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Activity budget and foraging behaviour of the Red squirrel (*Sciurus vulgaris* Linnaeus, 1758) in a coniferous habitat

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Abstract

The daily and seasonal activity-pattern, habitat use and foodchoice of free-ranging red squirrels (*Sciurus vulgaris* Linnaeus, 1758) were studied over a one year period using radio-telemetry. The daily activity-rhythm changed over the year. In winter squirrels were only active for a few hours, emerging from the drey with first light. Their activity was concentrated towards foraging, feeding mainly on high-energy seeds of pines. The large amount of time spent in the nest reduced the energy-costs of thermoregulation in cold weather. In spring the active period progressively expanded throughout the afternoon. This increase in the time spent active per day was probably caused by changes in environmental factors, such as increasing daylength and temperature, and a decreasing abundance of primary food-resources. From May to October the activity-pattern of the whole population was bimodal. Most likely endogenous factors, related to the depletion of the stomach content, form the basis of this bimodal pattern. Relating external factors to the length of the active phase, it was shown that daylength and temperature played an important role, being able to explain 93 % of the variation in the length of the active period throughout the year. Undoubtedly feeding-requirements are also of importance.

Introduction

Like most other tree-squirrels the European red squirrel (*Sciurus vulgaris* Linnaeus, 1758) is a diurnal animal, which offers the possibility to study its activity-pattern and behaviour through field observations. Some general information is available about activity and food-preference of red squirrels from direct field observations (Shorten 1962; Pulliainen 1973; Zwahlen 1975; Tittensor 1977; Wauters 1984), or from stomach-contents analysis of shot animals (Degn 1974; Tittensor 1977; Gronwall 1982). These studies show that, in general, red squirrels have a long and bimodal pattern of activity in summer, a short unimodal pattern in winter, and an intermediate pattern in spring and autumn. Their foraging-behaviour is concentrated on high-energy food resources, especially tree-

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seeds (of coniferous and deciduous trees). It is shifted towards alternative food-items such as fungi, buds, shoot, flowers and even animal matter when seeds are scarce or no longer available (see also Moller 1983).

It is assumed that the 24-hours activity rhythm exhibited by the red squirrel has an endogenous basis, as is the case in most other mammals (Aschoff 1963). However still little is known about the influences of environmental factors on the rhythm and the pattern of activity.

Tonkin (1983) examined the variation in the activity-pattern and foraging behaviour throughout the year and its relation to environmental factors in a deciduous wood, using radio-tracking. This paper presents a comparable study where it is tried to quantify the activity-budget of radiotagged squirrels in a coniferous habitat, and where the influences of environmental factors and behaviour on the patterns observed are examined.

Study area

A study area of 40.5 ha was chosen in a large coniferous wood (212 ha) at Herenthout, Province of Antwerpen, Belgium. It was dominated by Scots pine, *Pinus sylvestris* and Corsican pine, *Pinus nigra* var. calabrica (72 %), with some larch, *Larix decidua* (7 %) and a few mixed plots of oak, *Quercus robur* and beech, *Fagus sylvatica* (15 %). A detailed vegetation-study of the different plots had been carried out previously (Wauters 1984).

Material and methods

Field work

Between May 1985 and May 1986, twenty-eight different squirrels, 14 males and 14 females, were tagged with radio-transmitters (squirrel transmitter from Biotrack, U.K.). Each squirrel carried a transmitter for 1 to 5 months. In any one month eight to nine squirrels were monitored.

Two types of radiotracking techniques were used, i.e. radiosurveillance and point-fixes.

1. radiosurveillance: a tagged squirrel was located and then followed and observed for about one hour.
2. point-fixes: the radio-tagged squirrel was located and monitored for 5 minutes.

For both methods the following information was recorded every minute:

a. Foraging-place: i.e. the tree-species on which the squirrel was observed or the ground.
b. Height and substrate: a distinction was made between 4 height classes (0–5 m, 5–10 m, 10–15 m, > 15 m) and 3 substrate-classes (stem, large branches, small branches).
c. Behaviour: behaviour was assigned to one of the following categories 1. Foraging, including searching, handling and recovering stored food, 2. Food-storage behaviour, 3. Travelling, not related to foraging, 4. Interactions with other squirrels, 5. Grooming, 6. Resting outside the drey, 7. Other behaviour, 8. Not active, when sleeping or resting in the nest.
d. Remarks: additional comments about the observed behaviour when necessary, especially for categories 1, 4 and 7.
e. Position: all locations were mapped using X, Y coordinates.

In addition to the radio-tracking data casual observations were made of other squirrels. The information recorded was the same as that noted for tagged animals.

For every observation day some characteristics of the weather were noted: I. Proportion cloud-cover (0/8 to 8/8 scale), II. rainfall (none, slight, heavy, snow), III. wind-direction and wind-force, IV. Temperature (at 12.00 hours).

Data analysis

Although data were recorded on a one minute basis, the time-unit was further subdivided when necessary. Therefore data could be treated as monitored continuously.

Foraging place, substrate and height

The time spent on each tree-species or on the ground was expressed as a percentage of the total hours of active behaviour observed in each month. Data on the substrate used and the height-classes were treated the same way. It must be mentioned that the latter were not recorded for all observations.

Activity

The daily activity pattern of each month was deduced from all data collected that month using both radio-tracking methods. For each hour of the day all the time spent active was summed as was the time spent in the drey. The amount of activity per hour was expressed as a percentage, using the following formula:

$$\text{percentage activity/hour (A)} = \frac{\text{time spent active} \times 100}{\text{time spent active} + \text{time in drey}}$$

The mean number of hours of activity per day for each month was then calculated the following way:

$$\text{time active per day} \sum_{i=1}^{n} \frac{Ai}{100}, \text{ with n = number of hours activity recorded.}$$

As regards the activity-budged of the squirrel, the time allocated to each of the behavioural categories was expressed as a percentage of the total time spent active in each month.

Foraging-behaviour

Since foraging was quantatively the most important type of behaviour it was examined more closely. The percentage of time spent searching for and handling different food-items was estimated on a monthly basis, so that changes in the diet could be detected.

Results

Activity rhythm

The activity rhythm varied considerably over the year (fig. 1). From December to February activity started somewhat before sunrise (fig. 3), with a peak in the first hours after sunrise. The number of hours spent active per day during this period was less than five (table 1). The percentage of daylength when squirrels were active was lowest in February (48,4 %, table 1).

In early spring (March–April) squirrels still left their dreys at first light (fig. 2), but now activity lasted much longer. There was still only a morning peak, but the active period progressively expanded in the afternoon (fig. 1). In May the activity-rhythm showed a bimodal pattern, with an intense peak starting soon after sunrise, and a less pronounced and shorter one in late afternoon (fig. 1). In this month the number of hours of activity per day (10h06′) was the highest of the whole year (table 1). From May to September the pattern stayed bimodal, but the percentage of afternoon activity was variable (fig. 1). The largest amount of afternoon activity was found in July (48 %) when peaks were also less pronounced and there was little synchrony between start or offset of activity for different squirrels.

In October and November afternoon activity became less important (fig. 1). Nevertheles November was the month with the highest proportion of available daylight hours spent active (72 %) and the only one in which activity lasted till after sunset (fig. 2). Although it has been shown that the activity-rhythm often has an endogenous basis for mammals (Aschoff 1963), environmental factors were proven to be of great importance in squirrels (Pulliainen 1973; Zwahlen 1975; Pauls 1979; Tonkin 1983). Therefore we related the onset of activity to sunrise and offset of activity to sunset (fig. 2). We found that during the period when daylength was shortest (October to April), squirrels became active soon after first light, thus somewhat before sunrise. In the long summer months there was more than one hour difference between daybreak and the onset of activity (fig. 2). The relation between the end of the active period and sunset was less pronounced. Only in autumn and in May activity may have been ended through nightfall (fig. 2).

Variation in daylength and temperature contributed both to the variation in the length of the active period (table 1). The multiple correlation coefficient was highly significant (r =

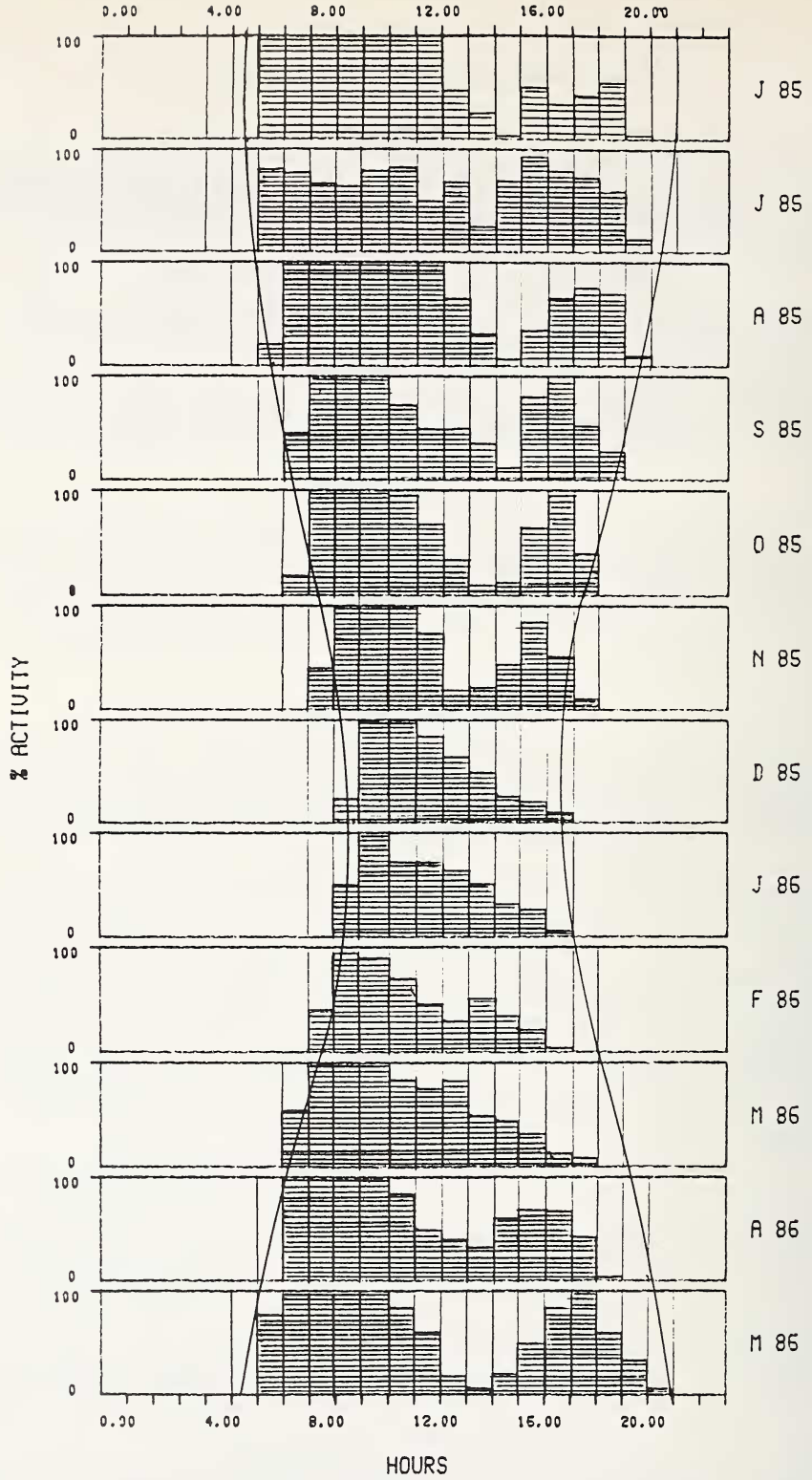

Fig. 1. Activity rhythm over a whole year. The times of sunrise and sunset are indicated by the curves. Radiotracking data were obtained for those hours marked as vertical blocks

Table 1

Daylength, mean monthly temperature, mean time spent active per day per squirrel, percentage of daylength spent active, time spent active in the afternoon per day, and afternoon activity as a percentage of total daily activity

Month	Mean hours between sunrise and sunset	Mean monthly max. t° (°C)	Mean monthly min. t° (°C)	Number of hours active per day			
				n	total %	n	afternoon %
1985							
May	15h29	18.0	8.9	10h10	65.7	4h36	45.2
June	16h28	18.2	10.3	9h38	58.5	2h38	27.3
July	16h06	22.5	13.0	9h59	62.0	4h49	48.3
Aug.	14h37	21.0	11.6	9h39	66.0	3h39	37.8
Sept.	12h41	19.1	9.7	7h49	61.7	3h36	46.0
Oct.	10h48	14.4	6.5	6h22	59.0	2h35	40.5
Nov.	9h00	5.5	0.3	6h28	71.9	2h20	36.0
Dec.	7h58	7.9	3.6	4h55	61.7	1h48	36.5
1986							
Jan.	8h26	5.0	−0.1	4h43	56.0	1h46	37.5
Febr.	9h58	−0.2	−6.8	4h50	48.4	1h22	28.4
March	11h48	9.0	0.6	7h29	63.4	2h21	31.4
April	13h47	10.2	2.7	8h28	61.5	3h05	36.4
May	15h29	18.9	8.5	10h06	65.2	4h03	40.1

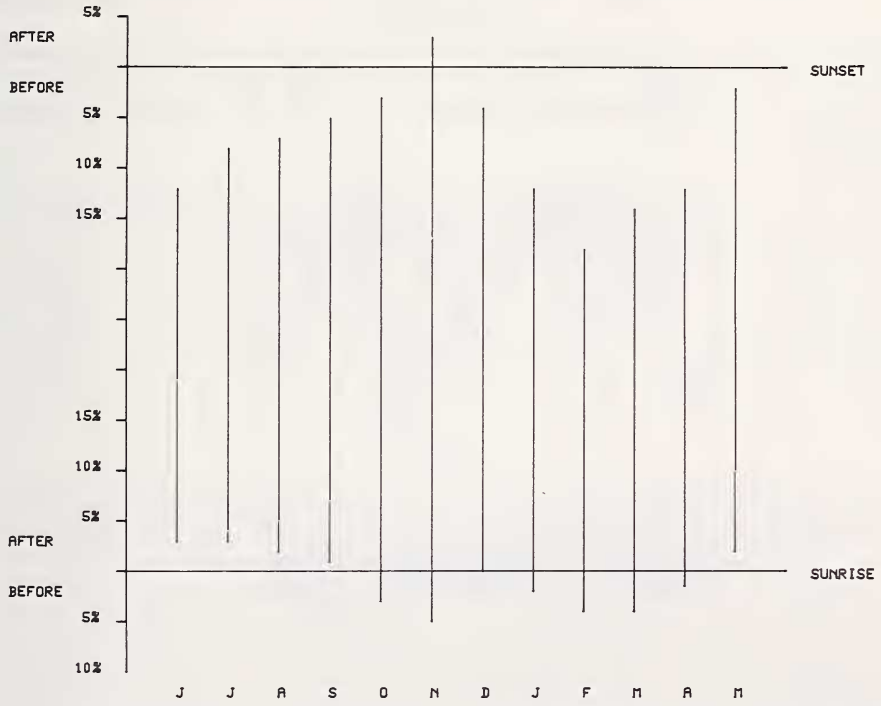

Fig. 2. Start and offset of activity related to sunrise and sunset. The time interval between start of activity and sunrise and between end of activity and sunset is expressed as a percentage of daylength for each month

0.966; F = 63.43; df = 2, 9; $p < 0.01$). Squirrels had a longer activity period when days are longer (partial correlation coefficient r = 0.958; $p < 0.01$) or when temperature is higher (r = 0.855; $p < 0.01$).

Activity budget

The major proportion of active time was spent foraging. It stayed fairly constant over the year, varying between 63 % and 78 % of total activity (table 2). There was however a difference in the proportion foraging time between the spring-summer (April–September) and the autumn-winter period (October–March), showing a tendency towards relatively more time spent foraging in the latter (table 3). In contrast other types of behaviour became more important in the spring-summer period.

Travelling, which always accounted for more than 10 % of the activity (table 2) was observed most in summer (table 3). Movements seemed nearly always to be direct, whether they were between feeding-sites or towards dreys. To test that the proportion of time available to squirrels for searching and handling food, was influenced by the proportion travelling time, a rank correlation was calculated between the monthly percentages foraging time and the monthly percentages travelling time. A statistically significant negative correlation was found (Spearman rank correlation; r = −0.736; n = 12; $p < 0.02$).

Squirrels groomed themselves throughout the year (table 2). However this behaviour was also observed more often in the spring summer period (table 3).

Table 2

Activity budget of radiotagged squirrels. Percentage behaviour classes comprising total monthly observed activity

Month	June 1985	July	Aug.	Sep.	Oct.	Nov.	Dec. 1985	Jan. 1986	Feb.	March	April	May
Sample size	17h36	22h33	24h37	16h25	27h17	25h35	22h00	22h48	22h43	32h50	19h35	31h35
Radiotagged squirrels	10	9	9	9	8	8	8	14	9	9	8	10
Behaviour	% of total time spent active											
Foraging	62.8	66.9	71.3	64.2	72.5	74.0	78.0	77.7	75.1	75.4	68.4	72.6
Seed-hoarding	–	–	0.3	3.3	3.7	2.5	0.8	0.3	–	–	–	–
Travelling	18.7	17.1	16.3	18.1	14.3	15.4	12.6	12.3	14.3	14.0	19.4	14.1
Interactions	0.8	0.4	0.4	0.7	0.6	0.8	0.5	0.3	0.2	0.9	0.8	0.7
Grooming	6.2	5.3	3.8	5.0	2.7	2.6	2.1	2.2	2.3	2.7	2.7	3.2
Resting	5.4	5.1	4.8	4.6	3.5	2.0	2.5	2.9	3.2	4.0	4.1	5.7
Mating chases	–	–	–	–	–	–	–	1.5	1.1	–	–	1.1
Others	6.1	5.2	3.1	4.1	2.7	2.7	3.5	2.8	3.7	3.0	4.6	2.6

Table 3

Mean percentage of different behaviour classes in summer and winter, calculated from table 2. A Mann-Whitney U-test was performed to compare the proportion of time spent on each behaviour class between the summer (April–September) and winter (October–March) period

Behaviour	% of total activity in summer (n = 6)	% of total activity in winter (n = 6)	U-value of Mann-Whitney U-test
Foraging	67.7 (+ 3.9)	75.5 (+ 2.1)	U = 1 (P = 0.002)
Travelling	17.3 (+ 1.9)	13.8 (+ 1.2)	U = 3 (P = 0.008)
Grooming	4.4 (+ 1.3)	2.4 (+ 0.3)	U = 1 (P = 0.002)
Resting	5.0 (+ 0.6)	3.0 (+ 0.7)	U = 0 (P = 0.001)

Grooming occurred regularly during the day, taking less than a minute up to a maximum of about 3 minutes. The longer grooming-sessions were performed mainly after emerging from the drey. Dozing occurred also significantly more in summer than in winter (table 3). It was seen most frequently from May till August (table 2), during the months when the absolute time spent active was highest (table 1).

While dozing, which took from a few to about 20 minutes, squirrels were seen using different postures according to varying weather conditions. In extreme conditions (heavy, cold winds, or very hot weather) they held the tail folded over the back, while in less severe weather they often let it hang down.

Some types of behaviour were only seen during certain seasons. This was the case for seed caching behaviour in autumn (table 2). Mating-chases only take place in the reproductive period. In 1986 females came into oestrus late January (unpublished data) and mating-chases were observed in January and early February (table 2). The second mating period started in May, when again males were seen chasing females.

Interactions between squirrels not related to reproductive behaviour never seem to be numerous, although they occur regularly. The fact that they are only short, from less than a minute to 3 minutes, is partly responsible for the low percentages of total activity they comprise (table 2). Expressed in absolute time, interactions only account for 35'' per day in February to a maximum of 4'37'' per day in June. The variation in the amount of aggressive interactions between months is rather small and these data do not allow to distinguish different periods when squirrels are more or less aggressive, although other data suggest these differences exist (Wauters and Dhondt 1985; Wauters 1986).

Habitat use

Since the study-area consists mainly of Scots and Corsican pine, these two tree-species were most used by squirrels (fig. 3). Furthermore oak was used regularly during certain seasons. Although larch and beech were also present in most parts of the wood, squirrels

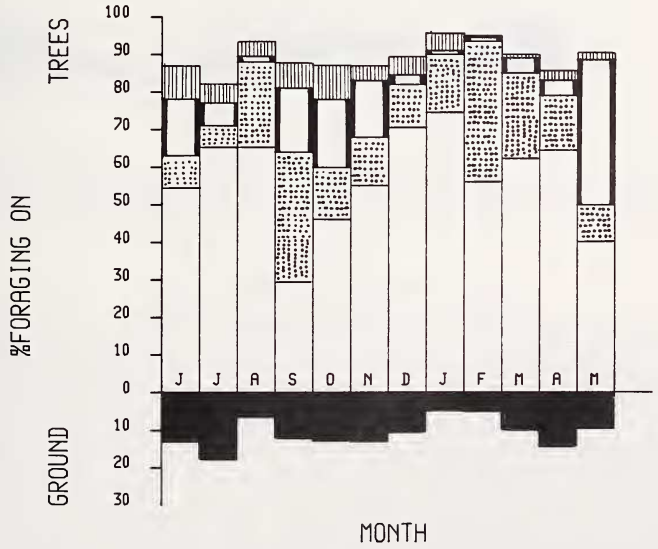

Fig. 3. Seasonal variation in habitat use of radiotracked squirrels. Percentage of total time spent active on different treespecies and on the ground. Scots pine □, Corsican pine ▦, oak ▢, other tree-species ▥

were only occasionally observed foraging on them (fig. 3). The time spent in oak-trees showed extreme seasonal variation, related to the temporal availability of different food-items.

From May to early July, which is the period between two successive cone crops, pines were used less compared to the rest of the year (fig. 3). The pines had shed their seeds by late April–early May, and it was not until the second half of June that new cones were taken. Differences in use between both dominant pine-species can be explained by the higher abundance of the Scots pine and by the fact that the Corsican pine had a much lower seed-crop that year (unpublished data). The differences were most extreme in June and July because the cones of the Corsican pine took longer to grow than those of the other species, and therefore were used only about a month later. Squirrels foraged a considerable amount of time on the ground in autumn, in April and early summer (fig. 3).

Looking at the different parts of the tree used by squirrels (fig. 4), we see that foraging was mainly observed on small branches, as we would expect since most food is found there. Large branches, especially those of oak, were used somewhat more in June and July, related to food-searching behaviour. The trunk of the tree is mainly used for travelling to and from the ground and therefore climbed on more often when squirrels spent more time on the ground (fig. 4).

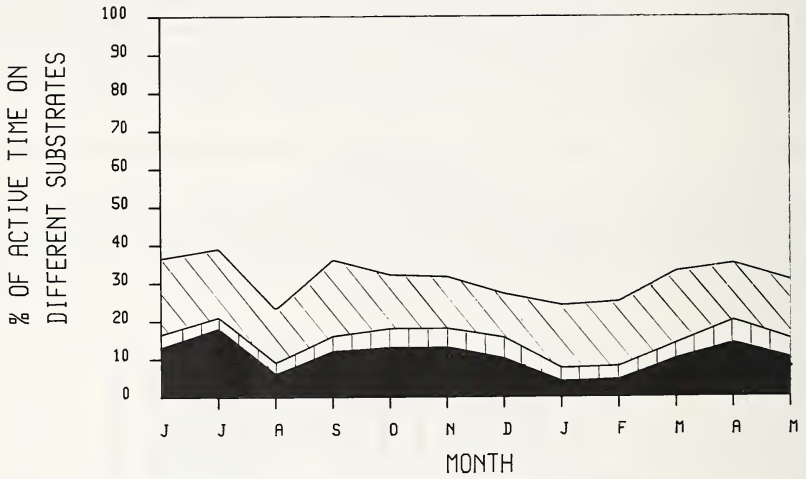

Fig. 4. Foraging substrate of squirrels in a coniferous wood. Percentage of active time spent on the ground and on different parts of the tree. Ground ■, trunk ▥, large branches ▧, small branches □

Foraging behaviour and food-choice

Foraging behaviour was further analysed, expressing the time used for searching and handling different food-items as a proportion of total time spent foraging (table 4).

Early June 1985 the diet was still diverse with 5 food-items comprising more than 4 % each. About 20 % of the time was spent in oak trees searching and eating caterpillars (11.1 %) and investigating dead branches for insect and fungi living under the bark (7.3 %). Squirrels were still regularly found foraging on the ground (18.2 %) where they searched for the remaining seeds in fallen pine-cones, or dug up their last food-reserves. The most important food was already found in Scots pine, with male flowers eaten early June (10.4 %) and already starting on the new green cones of the 1985 seed-crop the second half of the month (40.4 %). From July onwards till April of the next year pine seeds became the most important food-resource (table 4), with for Scots and Corsican pine together max-

Table 4

Seasonal variation in feeding-behaviour of radiotagged squirrels. Searching and handling food-items expressed as monthly percentages of observed foraging time

Month	June 1985	July	Aug.	Sep.	Oct.	Nov.	Dec. 1985	Jan. 1986	Feb.	March	April	May
Sample size	11h03	15h05	17h39	11h04	20h47	19h34	17h20	17h47	17h04	24h45	13h23	22h53
Feeding-behaviour	% of total foraging-time											
Ground	18.2	19.8	6.2	15.2	14.7	15.8	11.6	4.4	6.0	11.2	16.0	10.8
Searching	4.8	3.0	2.3	4.0	5.8	5.6	4.3	1.9	2.9	3.7	4.5	4.0
Fallen and cached Pine cones	12.8	3.9	–	1.1	1.2	1.9	1.5	1.0	2.1	4.1	8.0	4.2
Fallen and cached acorns	–	–	0.5	1.3	1.5	3.5	3.3	0.4	1.0	2.7	2.8	1.1
Berries	–	10.1	1.7	–	0.1	–	–	–	–	–	–	–
Fungi	–	1.3	0.9	3.9	1.3	1.4	0.8	–	–	–	–	0.2
Insects	0.6	1.5	0.8	–	–	–	0.7	0.7	–	0.7	0.7	1.3
Seed-hoarding	–	–	–	4.9	4.8	3.4	1.0	0.4	–	–	–	–
Corsican pine	5.4	1.1	18.3	33.4	12.4	13.7	11.8	14.1	36.9	21.7	13.9	6.34
Searching	0.6	0.6	1.9	1.4	1.0	1.6	0.8	1.2	3.0	2.1	3.0	1.6
Pine cones	1.7	0.3	16.4	32.0	11.4	12.1	11.0	12.9	33.8	19.4	8.8	1.1
Buds and shoots	0.9	0.2	–	–	–	–	–	–	–	0.2	1.6	3.3
Others	2.2	–	–	–	–	–	–	–	0.1	–	0.5	0.3
Scots pine	56.0	71.5	71.5	30.7	50.0	55.6	73.6	77.0	56.7	64.3	67.1	40.6
Searching	2.9	1.1	2.7	1.8	3.3	5.4	6.2	6.1	4.2	5.6	10.6	5.2
Pine cones	40.4	69.8	68.6	28.4	46.0	50.2	67.4	70.9	52.5	58.7	45.1	20.2
Buds and shoots	2.2	0.6	–	–	–	–	–	–	–	–	10.7	10.0
Male flowers	10.4	–	–	–	–	–	–	–	–	–	–	4.7
Others	–	–	0.2	0.5	0.7	–	–	–	–	–	0.7	0.5
Larch	0.8	1.3	0.4	0.2	1.7	0.9	0.2	0.1	–	0.2	–	0.2
Searching	0.3	0.4	0.2	0.1	0.5	0.4	0.1	0.1	–	–	–	–
Larch cones	0.5	0.9	0.2	0.1	0.7	0.5	–	–	–	–	–	–
Others	–	–	–	–	0.5	–	0.1	–	–	0.2	–	0.2
Spruce	–	0.6	0.9	1.2	0.8	0.4	1.6	3.9	0.3	0.3	0.7	0.8
Searching	–	0.3	0.3	0.1	0.1	–	0.4	0.7	0.1	–	0.2	0.1
Spruce cones	–	–	0.3	1.1	0.5	0.4	1.2	1.2	0.2	–	–	–
Buds and shoots	–	0.3	0.3	–	–	–	–	2.0	–	0.1	0.5	0.7
Oak	19.6	5.7	1.3	18.2	18.3	13.6	1.2	0.5	0.1	2.3	2.1	41.1
Searching	1.2	–	–	2.1	3.4	3.3	–	–	–	–	0.1	4.1
Acorns (+ cached ones)	–	–	0.4	15.5	14.6	9.3	1.0	0.2	–	1.0	0.5	0.7
Fungi and insects living Under the bark	7.3	1.4	0.9	0.6	0.3	1.0	0.2	0.3	0.1	1.0	1.5	1.6
Catterpillars	11.1	4.3	–	–	–	–	–	–	–	–	–	11.9
Flowers	–	–	–	–	–	–	–	–	–	–	–	22.4
Others	–	–	–	–	–	–	–	–	–	0.3	–	0.4
Others	–	–	1.3	1.3	2.1	–	–	–	–	–	0.2	0.2

imum percentages in January (91.1 %) and February (93.5 %). Some variation was brought into this homogenous but energy-rich diet with other, so called secundary, food-items. In July squirrels were eating berries of an abundant shrub-species, *Vaccinium myrtillus* (10.1 %), while mainly in September (3.9 %) and during the following months they searched the ground for fungi.

From September onwards acorns became an important part of the squirrels' diet (table 4).

Squirrels intensively foraged in the oak trees along the lanes during autumn, with searching and handling acorns comprising 17.6 % of total foraging time in September 1985, and still 12.6 % in November. When autumn progressed and more and more acorns were

shed, the ratio of searching time on handling time increased (0.14 in September, 0.35 in November, see table 4). By the end of November squirrels shifted their foraging behaviour, again concentrating mainly on coniferous trees.

During the same autumn period the squirrels spent a lot of time on the ground (table 4). Pine cones and acorns were bitten off and brought down where they were hidden in food-caches. This activity was performed mainly in September (4.9 %) and October (4.8 %). Rather a lot of the cached food was recovered soon after it was hidden. Therefore searching for and handling stored food comprised 8.5 % and 11 % of total foraging behaviour in October and November respectively (table 4).

During the winter squirrels concentrated their feeding-efforts on pine-seeds, until late March (table 4). From April onwards the diversity of the diet increased. Warm April days caused the bursting of cones and a large proportion of the seeds shed. Moreover cone density had decreased strongly by now, especially in Corsican pine where the 1985 cone-crop was poor. This resulted in a marked increase in the ratio of searching to handling time in Scots pine (0.10 in March, 0.24 in April and 0.26 in May) as well as in Corsican pine (0.11 in March, 0.34 in April and 1.45 in May)! Mainly buds of coniferous trees (12.8 %) were used in April, while in May the young shoots and male flowers became more important (12.2 %).

Squirrels found however the most suitable food-resource in flowering oak-trees. The oak flowers, abundant but only available for a short period of time, were the main food-item in this month, their handling time comprising 22.4 % of foraging time (table 4). By the end of the month flowers withered but now a new temporary food-resource became increasingly available, the emerging caterpillars. Up to 11.9 % foraging time was spent searching for the insect-larvae and eating them.

Discussion

The activity-rhythm that was observed resembled the results obtained for red squirrels in different parts of its distribution area (Ognev 1940 in the Soviet Union; Saint-Girons 1966 in France; Degn 1974 in Denmark; Purroy and Rey 1974 in Spain; Tonkin 1983 in Great-Britain). The bimodal pattern in summer, the unimodal activity-peak in winter and an intermediate pattern in spring and autumn was found in most cases. Nevertheless there seems to be some geographical variation and possibly variation related to the type of habitat. In the West of France (Saint-Girons 1966) squirrels stayed active throughout the day in winter, while in deciduous woods in England (Tonkin 1983) the early afternoon drop in activity during the summer months, found in this study, was not present. Mild weather in winter and a low abundance of energy-rich food in summer are environmental factors that might have caused this increase in the time spent active.

Combining our data on the activity budget, habitat use and changes in foraging behaviour allows us to explain the seasonal variation observed in the activity pattern.

Winter

From December to February squirrels emerge from the drey before sunrise with all individuals showing an activity-peak the first daylight hours. Total active period is short and about 18–19 hours per day is spent in the drey. A very high proportion of activity is spent foraging for energy-rich food resources. Pine seeds, which were very abundant this year, comprise more than 90 % of the diet, allowing the squirrels to have a high rate of food-intake. Therefore the energy-demands can be fulfilled in only a few hours of foraging. Staying active in cold weather causes severe heat loss and hence increases the energy-costs to maintain the body-temperature. Therefore hardly any time is spent on

other activities, such as grooming and resting, and squirrels reenter the drey around noon. Pulliainen (1973) showed that in Northern Scandinavia dreys are very important for thermoregulation. The temperature in a drey while a squirrel is in it is about 10 to 20 >C above air-temperature. Since related species (Golightly and Ohmart 1978) are heterothermic, showing a decrease in body temperature while resting in a nest, we can assume that in cold conditions, resting in the drey is an important behavioural response resulting in a decrease of the energy-costs of thermoregulation.

Spring

When spring progresses, the seed-crop of the coniferous trees gradually gets depleted, while warmer weather in late April causes the cones to burst open and shed their seeds. This decrease in the abundance of primary food-items forces the squirrels to spent more time travelling between good feeding-sites, and furthermore to increase the diversity of their diet. Buds, shoots, flowers and even insects become important food-items. The change in habitat use, with squirrels foraging more often on the ground looking for scattered food-stores, also increases travelling time. This shift in diet and activity-pattern causes a decrease in the rate of energy-intake and hence forces the squirrels to spend more hours active per day. Therefore activity gradually expands throughout the afternoon.

It is also shown here that changes in habitat use are closely linked with the presence of food resources that are locally abundant but only used for a short time.

Squirrels are concentrating their feeding efforts on oak flowers in May, shifting towards caterpillars in late May and June. This low-energy diet in May seems to be the major cause for the maximum in absolute time spent foraging (7h20′) which was observed in this month.

Summer

One of the aspects of the squirrels' activity-rhythm that remains a puzzle is the pattern becoming biphasic and staying that way in summer. Although this pattern is the one most commonly observed in animals (Aschoff 1966) its mechanism is not yet understood. Concerning its function in squirrels it very likely has something to do with thermoregulation. The summer resting phase in the drey occurs during the warmest period of the day, when staying active might bring the squirrels into overheating problems. Another possibility is that after the morning feeding period, the contents of the stomach reach capacity, and a break in activity is therefore necessary (Tonkin 1983).

Differences in physiological condition related to the stomach content may also be able to explain why in winter (after a long period without any food intake and a high cost of thermoregulation) activity starts with daybreak, while in summer (only a short night-rest without food-intake and a low cost of thermoregulation) it often takes an hour or more before squirrels emerge from the drey. This might be an important element of the endogenous basis of the activity-pattern.

The long active period (about 8 to 10 hours) is, apart from daylength, related to the activity-budget and food-choice. In summer squirrels spend an important amount of time resting outside the drey during which they take postures that seem to have a temperature-regulating function. Hence it is likely that dozing is a behavioural response to avoid overheating during the active period. Also grooming comprises more than 5 % of the activity-budget. The increasing grooming activity is most likely related to the higher amount of skin-parasites the squirrels suffer from, compared to the winter-period.

In early summer squirrels still need to travel a lot to find good feeding-places, or between scattered food-resources, leaving less time available for searching and handling the food. In June for example, they travel some 108 minutes per day against only 35 in January. Furthermore squirrels take, mainly in June and early July, still an important

amount of food-items with a low energy-content, such as the remaining seeds in fallen pine-cones, berries and insects. Therefore the rate of energy-intake is rather low, forcing the squirrels to forage for a longer time period. In July afternoon activity was most important, and the peaks were not very pronounced. This could be explained by the fact that at that time nearly all the radio-tagged squirrels were adult females, which had their litter born early July (Wauters and Dhondt 1985). During the first week of lactation they spent a lot of time nursing the young and often emerged from the drey several hours after sunrise. Not only the onset of activity was delayed, but also the synchronicity was lost, since different females left the drey at different times.

Autumn

In autumn the afternoon activity peak becomes less important, nevertheless the absolute time spent active stays around 6h30'. During this time of the year high-energy food is most abundant, which is reflected in the decrease of travelling time and the increase of feeding time. Squirrels temporarily shift their food-choice and concentrate on the seeds of deciduous trees, that are only available for a short period of time. In 1983 beech was regularly visited, harvesting the large beechmast crop while oak, which had a very poor acorn crop that year, was disregarded (Wauters 1984; Wauters and Dhondt 1986). In the autumn of 1985, with a crop failure in beech but an abundant crop for oak, they concentrated on the latter. Feeding only on energy-rich food-items the rate on energy-intake becomes very high. Furthermore the air temperature is not yet that low that squirrels would have high costs of thermoregulation, nor do they seem to have to perform behaviour to avoid extreme heat loss. It is also at this time of the year that their body-weight is highest (unpublished data).

Another response to the high abundance of temporary primary food-resources is food-caching behaviour, which has an important effect on food-availability later on. Hiding acorns decreases the intensity of interspecific competition with animals harvesting the seeds as soon as they have fallen to the ground. The caching of cones provides the squirrels with energy-rich food in the late spring period between two successive seed-crops. Stored in the damp upper-layer of the forest ground the cones remain closed and seed-shedding is delayed.

The data presented here on the proportion of each food-item in the diet, should be combined with quantitive data about the rate of energy-intake to enable us to calculate the daily energy-intake for each month.

Lab-experiments should be done, measuring the energy-costs of metabolism under different conditions allowing to calculate the energy-balance of the squirrel, and hence understand better the influences of environmental factors and certain types of behaviour on the squirrels' condition.

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Zusammenfassung

Aktivität und Verhalten bei der Nahrungssuche von Eichhörnchen (Sciurus vulgaris Linnaeus, 1758) im Nadelwaldhabitat

Der tägliche und jahreszeitliche Aktivitätsrhythmus, die Habitatnutzung und die Nahrungswahl von freilebenden Eichhörnchen *(Sciurus vulgaris)* wurden mit Hilfe von Radiotelemetrie in einem Nadelwald untersucht. Der tägliche Aktivitätsrhythmus änderte sich während des Jahres. Im Winter waren die Eichhörnchen nur wenige Stunden aktiv. Sie suchten am frühen Vormittag vor allem energiereiche Kiefersamen. Die lange Zeit, die sie im Nest bleiben, reduziert die Kosten der Thermoregulation. Im Frühling verlängere sich die Aktivitätsperiode allmählich, und die Tiere wurden auch nachmittags

aktiv. Dieses wurde wahrscheinlich durch Milieufaktoren verursacht, wie wachsende Tageslänge, zunehmende Temperatur und abnehmende Mengen von Baumsamen. Der Aktivitätsrhythmus der Population wurde bimodal. Für die monatlichen Mittelwerte erklären Tageslänge und Temperatur 93 % der Variation der Aktivitätsdauer.

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